Foraging habitats of top predators, and Areas of Ecological Significance, on the Kerguelen Plateau

by

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ABSTRACT. - Avian and mammalian predators play a key role in the Kerguelen Plateau ecosystem, both with respect to structuring the marine community and its response to anthropogenic influences, such as climate change and commercial fisheries. A powerful way to determine regions of particular ecological importance is to identify Areas of Ecological Significance (AES): regions that are utilized by multiple predator species. Such concentrations of foraging activity are indicative of enhanced primary and/or secondary productivity. These are regions that require specialised management efforts, and which are of considerable importance in the development of ecological models and climate monitoring systems. This study integrates tracking and diving data from a suite of predator species collected as part of both the French and Australian Antarctic programs at Kerguelen Islands and Heard Island respectively. Tracking and/or dive data for Macaroni and King penguins, southern Elephant seals, Antarctic fur seals and Black-browed albatross were analysed. The estimated path for each animal was derived using state-space models, which also allocated each location to either "transit" or "search" behavioural modes. For diving species, dive depth data were temporally allocated along the path, providing information on three-dimensional habitat use. Areas of Ecological Significance for each species and for the combined suite of predators were identified using Kernel Density analysis. The role of bathymetry, ocean circulation and other environmental factors underlying the AES were established using deterministic models, which can be used to predict predator foraging habitats across the entire plateau.

RÉSUMÉ. - Habitats d'alimentation et zones d'importance écologique des prédateurs supérieurs au niveau du Plateau de Kerguelen.

Les prédateurs que sont les oiseaux et mammifères marins jouent un rôle clef dans l'écosystème du Plateau de Kerguelen, d'une part en structurant la communauté marine et d'autre part dans leur réponse aux influences anthropiques tels que le changement climatique et les pêcheries commerciales. Un puissant moyen pour déterminer les régions d'une importance particulière en écologie est d'identifier les Aires d'Importance Écologique (AIE) : régions qui sont utilisées par un ensemble d'espèces de prédateurs. De telles concentrations relatives à l'activité d'alimentation sont indicatives de zones de productivité primaire et/ou secondaire accrues. Ces régions nécessitent des efforts de gestion particuliers et sont d'importance considérable dans le développement de modèles écologiques et des systèmes de suivi du climat. Cette étude incorpore des données de pistage et d'enregistrement des plongées d'une série de prédateurs récupérées tant lors de programmes français et australiens d'une part aux îles Kerguelen et d'autre part à l'île Heard. Les données de pistage et/ou les enregistrements des plongées concernant les manchots macaroni et royaux, les éléphants de mer, les otaries de Kerguelen et les albatros à sourcils noirs ont été analysées. Les trajets estimés pour chaque animal ont été déduits de modèles spatio-temporels lesquels attribuent aussi chaque position à un mode comportemental de type "passage" ou "recherche". Pour les espèces effectuant des plongées les données de profondeur de plongée ont été temporellement attribuées le long du trajet, fournissant une information de l'utilisation tri-dimensionnelle de l'habitat. Les Aires d'Importance Écologique ont été identifiées pour chacune des espèces ainsi que pour une série combinée de prédateurs en utilisant les analyses de densité de Kernel, Le rôle de la bathymétrie, de la circulation océanique et d'autres facteurs environnementaux sous-jacents à l'AIE a été établi en utilisant des modèles déterministes qui peuvent être utilisés pour prédire les habitats d'alimentation des prédateurs pour l'ensemble du Plateau.

Key words. - Marine predators - Foraging - Telemetry - Ecological significance.

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Top predators, such as birds and mammals, play an important role in marine ecosystems. They can be influential in structuring marine communities through top-down ecological processes (Ainley *et al.*, 2007; Lavery *et al.*, 2010), but equally can themselves be influenced by processes operating on lower trophic levels, such as changes in oceanographic processes (Laidre *et al.*, 2008), or commercial harvesting of prey species (Nicol and Robertson, 2003). Quantifying the at-sea distributions of predators is a powerful way of identifying regions that are particularly important ecologically (Block *et al.*, 2002), and this is particularly true for regions that are used by multiple species of predators, as this is indicative of not only relatively high abundance of prey, but also relatively high diversity of prey species. Concentrations of foraging activity are therefore indicative of enhanced primary and/or secondary productivity (Constable *et al.*, 2003; Hofmann *et al.*, 2008), and these are regions that are of considerable importance in the development of ecological models and climate monitoring systems (Constable *et al.*, 2000; Constable*, et al.*, 2003; Hill *et al.*, 2006; Hofmann*, et al.*, 2008).

Kerguelen Islands and Heard Island are isolated land masses lying on the Kerguelen Plateau. This isolation means that the islands are the only breeding sites for birds and seals in that sector of the Southern Indian Ocean, ensuring high densities of penguins, petrels and seals. These animals therefore, are a significant component of the ecosystem in the surrounding oceans, including the Kerguelen Plateau (Weimerskirch *et al.*, 2003). The plateau is one of only two bathymetric obstructions to the eastward movement of water in the Southern Ocean (the other being the Drake Passage), and as such, is a region of complex bathymetry and oceanography (Park *et al.*, 2008b; Park and Vivier, this volume). This is manifested in the dynamic splitting and merging of the Antarctic Polar Front, local regions of upwelling, and downstream enrichment of productivity due to iron enrichments from the land masses (Park *et al.*, 2008a; Park*, et al.*, 2008b; Mongin *et al.*, 2009; Park *et al.*, 2009).

The oceanographic processes associated with the plateau result in regional enhancement of primary productivity, flowing up to abundant populations of zooplankton, squid and fish. Avian and mammalian predators, as well as commercial fisheries, exploit these prey, giving the Kerguelen Plateau an abundant and diverse community of top predators. The diets of the predators have be studied in some detail; some, such as Antarctic fur seals, *Arctocephalus gazella* (Peters, 1875), take a variety of fish, primarily Channichthyidae and Myctophidae, although this varies both spatially and temporally (Lea *et al.*, 2006; Casper *et al.*, 2007; Goldsworthy *et al.*, 2010), others specialise in zooplankton (Bocher *et al.*, 2001), while others take a more mixed diet, for example Macaroni penguins, *Eudyptes chrysolophus* (Brandt, 1837), which feed on both euphausiid crustaceans and myctophid fish (Deagle *et al.*, 2007).

The foraging behaviour of the predators in the region have also been relatively well studied, confirming the importance of the plateau as a foraging area, particularly during the breeding season when land-breeding predators have restricted foraging ranges due to the need to regularly nourish their young. For example, Antarctic fur seals, have been studied at multiple colonies at both Kerguelen Islands and Heard Island (Lea *et al.*, 2008; Casper *et al.*, 2010; Goldsworthy *et al.*, 2010), and are known to forage in areas of relatively high Chlorophyll-*a* concentrations on the plateau, associated with fronts and bathymetric features such as Gunnari Ridge east of Heard Island (Guinet *et al.*, 2001; Lea *et al.*, 2006). Similarly, the plateau is important to King penguins, *Aptenodytes patagonicus* (Miller, 1778), which also focus their foraging behaviour in the region of oceanographic fronts and eddies (Charrassin and Bost, 2001; Cotté *et al.*, 2007).

Some marine predators are specialist divers, hunting well below the ocean's surface (Hindell, 2008). Southern Elephant seals (*Mirounga leonina*, Linnaeus 1758) are an extreme example of this, routinely diving to depths in excess of 1000 m and being submerged for up 90% of their time at sea (Hindell *et al.*, 1991; Bailleul *et al.*, 2008). Penguins and Fur seals, while not diving to these extremes, still forage at depth, often below the mixed layer depth (Bost *et al.*, 2002; Charrassin *et al.*, 2004). This introduces a third dimension to any consideration of habitat for marine predators, and can be particularly important when attempting to model habitat use as the conditions encountered at depth can be quite different to the surface conditions measured by oceanographic satellites (Gremillet *et al.*, 2008).

Due to the considerable number of tracking studies of individual species in the region, it is now possible to combine these to identity regions that are used intensively by the community of predators. We regard these as Areas of Ecological Significance (AES), which are defined as important foraging regions for multiple species of predators. Even without further data on distribution and abundance of lower trophic levels, these regions which support a diversity of predators, are likely to be indicative of relatively high levels of abundance and biodiversity. The aim of this study is to integrate tracking and diving data from a suite of predator species collected as part of both the French and Australian Antarctic programs in the last decade. Specifically, the study aims to (i) develop a technique for identifying AES on the Kerguelen Plateau, (ii) investigate whether these could be described by oceanographic or other parameters, and (iii) examine the importance of the vertical dimension in the definition of AES.

METHODS

Overview of location data

The study has drawn on satellite tracking and dive behaviour data from five of the most common avian and mammalian predator species on the Kerguelen Plateau. These were southern Elephant seals, Antarctic fur seals, King penguins, Macaroni penguins, and Black-browed albatrosses (*Diomedea melanophrys*, Temminck, 1828). All animals were equipped with an Argos platform transmitter terminal (PTT), providing up to 15 surface locations per day. With the exception of the Black-browed albatross, a number of individuals of each species also carried time depth recorders (Wildlife Computers, Redmond, WA, USA) to provide concurrent data on diving behaviour. For the Elephant seals, both location and dive depth data were provided by Sea Mammal Research Unit Satellite Relayed Data loggers (SMRU-SRDLs, St. Andrews, Scotland, UK).

Overall, 343 individual animal tracks were incorporated in the analyses, although the number of species, individuals, as well as the colonies studied, varied among and within Heard Island and Kerguelen Islands populations (Tab. I). Data from four species were acquired from Heard Island, collected on the 2000-2001 and 2003-2004 Australian Antarctic expeditions (Tab. I). Only data from southern Elephant seals, Antarctic fur seals and King penguins were used from Kerguelen Islands. These were collected between 1996 and 2008 by participants of the French Antarctic programme, and have been described in detail elsewhere (Guinet, *et al*., 2001; Lea and Dubroca, 2003; Bost *et al*., 2004; Charrassin *et al*., 2004). There were too few data to account for inter-annual differences for all of the species in the analyses.

The start and end date and time of the first foraging trip were identified for each track. This enabled the exclusion of on-land locations which would tend to inflate the relative importance of the colonies in subsequent analyses, and also ensured that no individual has undue influence on the overall distributions by making multiple trips. The most probable paths of the animals during these trips were then estimated using state space models (SSMs) (Jonsen *et al*., 2005; Patterson *et al*., 2008), which use the Argos position accuracy estimate, the rate of travel, and turning angle in a hidden Markov framework. This will estimate the most likely position of each location, the probability of the animal being in either a search or transit behavioural mode, and returns locations in regular time intervals. A two-hour time interval was used throughout to ensure consistency in the number of locations per day among species.

Identification of AES

Areas of Ecological Significance on the Kerguelen Plateau region were defined as:

Areas used for foraging rather than migratory corridors

For this, we used the behavioural states identified by the state space models, and restricted analysis to locations in the "search" mode (i.e., when the animal was travelling relatively slowly and making many changes in direction between locations).

Areas used by many individuals

To identify areas visited most intensively by the animals, we produced kernel density maps using *Eonfusion V2.0* (Myriax Pty. Ltd., Hobart, Australia). Kernel densities provide contoured representations of the densities of at-sea locations, and as such are sensitive to the number of locations used in the analysis. This is a problem when combining data from different sites, or different species, for which there are differing number of animals tracked, as the site or species with the most locations will dominate the kernels. We used the tracks derived from the state-space models described above, with a two-hour time interval, to ensure a constant number of locations per day for each individual. For the combined analysis of all species from both islands, we also weighted the number of locations used for each species to ensure that species with relatively few tracks were given

Table I. - The number of individuals equipped with satellite transmitters and time depth recorders (in parenthesis) used in the study. The deployments are summarised by species, island and colony.

Island	Colony	Black-browed Albatross	Antarctic Fur Seal	King Penguin	Macaroni Penguin	Southern Elephant Seal	Total
Heard	Capsize Beach	0	0	0	85 (85)	0	85 (85)
Heard	Roger's Head	10	0	0	20	0	30
Heard	Spit Bay	0	64 (55)	49 (25)	0	0	113 (80)
Kerguelen	Cap Noir	0	49	0	0	0	49
Kerguelen	Iles Nuageuses	0	5	0	0	0	5
Kerguelen	Courbet Peninsula	0	0	0	0	19 (19)	19
Kerguelen	Pointe Suzanne	0	33	0	0	0	33
Kerguelen	Ratmanov	0	0	9	0	0	9
Total		10	151	58 (25)	105 (85)	19 (19)	343 (165)

equal representation in the kernels to species with large numbers of tracks. This was achieved by taking a random subset of 5 393 "search" locations for each species. This was determined by the number available for Black-browed albatross, the species with fewest data points.

Areas used by multiple species

We calculated species richness values for each 10 x 10 km grid within the Kerguelen plateau region. These were derived using the weighted locations also used in the kernel density analysis, and were simply a count of which species had locations within each 10 km^2 grid. The size of the grid was a trade-off between being too small, thereby reducing the likelihood of locations from multiple species falling within it, and being too large, thereby having a large number of grids with the maximum number of species.

We then used those grids with species richness of at least four, and relative densities of 0.9 (i.e., Kernel densities in the top 90 percentile of the distribution) to identify AES.

Relationship to environmental parameters

Once the AES were identified, we modelled their relationship to a suite of biological and environmental parameters. The biological variables were: distance of the AES grid to the animal's tagging site (*Dist0*) and the distance to the 1000 m bathymetric contour (*Dist1000*), which was taken to be an indication of the shelf break. The environmental variables were: weekly sea surface temperature (*SST*, NOAA Optimum Interpolation Sea Surface Temperature V2, weekly average at 1° x 1° resolution, http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html), sea surface height anomaly (*SSHa*, daily AVISO Gridded Sea level anomalies, 1/3°x1/3° resolution, http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/global/index.html), and bathymetry (*ocean-d* using GEBCO 30 second data).

We used a general linear model (GLM) with a binomial error distribution and logit family, to model whether a 10 km^2 grid was an AES, or not, based on the criteria described above. We ran a number of candidate models, including all terms on their own and in all possible additive combinations. The resulting models were compared using delta Akaike's Information Criterion (ΔAIC).

Three-dimensional habitat description

With the exception of Black-browed albatross, all of the species included in this study are divers. Therefore, it is likely that environmental variables measured on the surface may not be an accurate reflection of factors that influence the distribution and abundance of prey at depth. We investigated the depth component of each species' distribution qualitatively by calculating horizontal Kernel density maps at 10 equally spaced depth intervals. These Kernel densities were derived by randomly selecting individual depth records from all available TDR records for each species. In order to ensure a similar density of depth points between individuals and species, we re-sampled the depth data at a rate of approximately once every 200 s (the density of points in the Elephant seal data which had coarsest temporal resolution). These depths were then merged to the individual's track data using a linear interpolation between the SSM derived two-hourly location estimates, and combined for each species. The resulting three-dimensional cloud of points was then divided into ten equally spaced horizontal slices and a Kernel density calculated for each slice. Finally, we calculated two three-dimensional iso-surfaces (density envelopes) that enclosed the 50 and 90 percentiles components for these kernels. Data manipulations and visualisations were performed in *Eonfusion* software.

RESULTS

Species specific usage

Southern Elephant seals

We included data from 21 seals, all tagged post-moult on the east coast of Kerguelen Islands (Bailleul *et al*., 2007b; Charrassin *et al*., 2008). Nineteen of these were juvenile males (mass range 300-1100 kg), and were part of a total of 47 seals in this age group that were tagged between 2002 and 2008. The other two seals were adult females. Only seals that spent part of their post-moult foraging trip over the Kerguelen plateau were included. The majority of the locations were collected between January and May, although a small number of locations were also collected each month for remainder of the year (Fig. 1a).

The locations were widely dispersed over the Kerguelen Plateau. The Kernel density analysis indicated that highest concentrations of locations occurred within the 1000 m bathymetric contour. There were also a number of regions of particularly high concentrations. These were all to the east and southeast of Kerguelen Islands, and many were associated with the shelf break.

Black-browed albatrosses

These data were from ten individuals, all tagged at Heard Island between December 2003 and February 2004 (Lawton *et al*., 2008). The majority of the locations were associated with the southern shelf break to the south and east of Heard Island (Fig. 1b). This is a region of complex bathymetry, including a number of canyons and ridges. There were several other locations of concentrations, associated with the shelf break to the north of Heard Island.

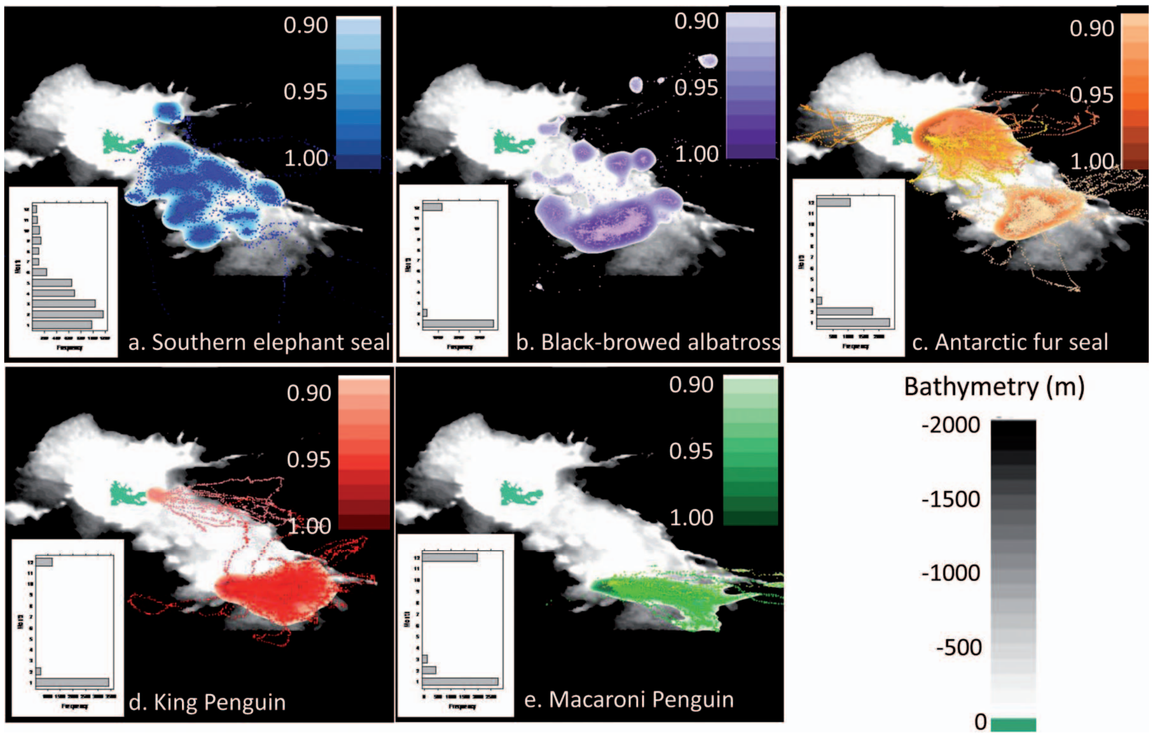

Figure 1. - Kernel density estimates for each of the four predators used in the study, based on the two hourly time step locations derived from state space models.

Antarctic fur seals

We included data from 151 seals, all adult females, tagged at five sites (Tab. I), three at Kerguelen Islands and two at Heard Island (Guinet *et al*., 2001; Lea *et al*., 2006; Lea *et al*., 2008; Goldsworthy *et al*., 2010; Staniland *et al*., 2010). The deployments were all made between December and March corresponding to the breeding season for this species in eight years from 1998 to 2009. The individual tracks indicate that some individuals moved past the 1 000 m contour to forage over deep oceanic waters (Fig. 1c). However, the kernel density analyses showed that 90% of all locations were over the Kerguelen Plateau and shelf break. There was a general pattern of the seals spending time to the east of their breeding colonies, with areas of highest densities lying immediately to the north east of Kerguelen Islands and to the east and northeast of Heard Island. The Heard Island seals also used the shelf break to the south and east of the island, the same area as used by the Black-browed albatross. The few seals tracked from île de Croy, in the northwest of the Kerguelen group, were the exception, as they all moved westwards past the 1000 m bathymetric contour.

King penguins

Data from 58 king penguins were incorporated in the analyses, when all breeding birds were tagged in the summer months (Tab. I). The majority of the instrumented birds were from Long Beach on the eastern side of Heard Island (Wienecke and Robertson, 2006), but nine were also tagged at Ratmanov Beach on the eastern side of the Courbet Peninsula at Kerguelen Islands (Charrassin *et al*., 2004). As with the Fur seals, although some individuals moved off the plateau to feed in oceanic waters, the bulk of the locations were within the 1 000 m contour, and to the east of the breeding colonies (Fig. 1d). The region of high use to the east of Heard Island was larger and more diffuse than for the Fur seals, and while the shelf break was used, the highest densities of locations were directly east of the island.

Macaroni penguins

We only used data from Heard Island in the analyses, and these were breeding birds tagged at either Roger's Head on the western side of the island in 2000, or at Capsize Beach in the southeast in 2003-2004 (Tab. I). Birds from both colonies moved to the east of the island with the majority of birds remaining over the 1000 m contour (Fig. 1e). There were however aggregations of locations beyond this, indicating that the oceanic waters are important to this species at some points in the breeding season. More than any of the other species in this study, Macaroni penguins, have pronounced variation in their foraging trip durations throughout the breeding season. Early in the summer, when parents are taking turns to brood small chicks (the guard stage), foraging trips are short, often less than 24 hours, thereby constraining foraging to the region relatively close to shore (Deagle *et al*., 2007).

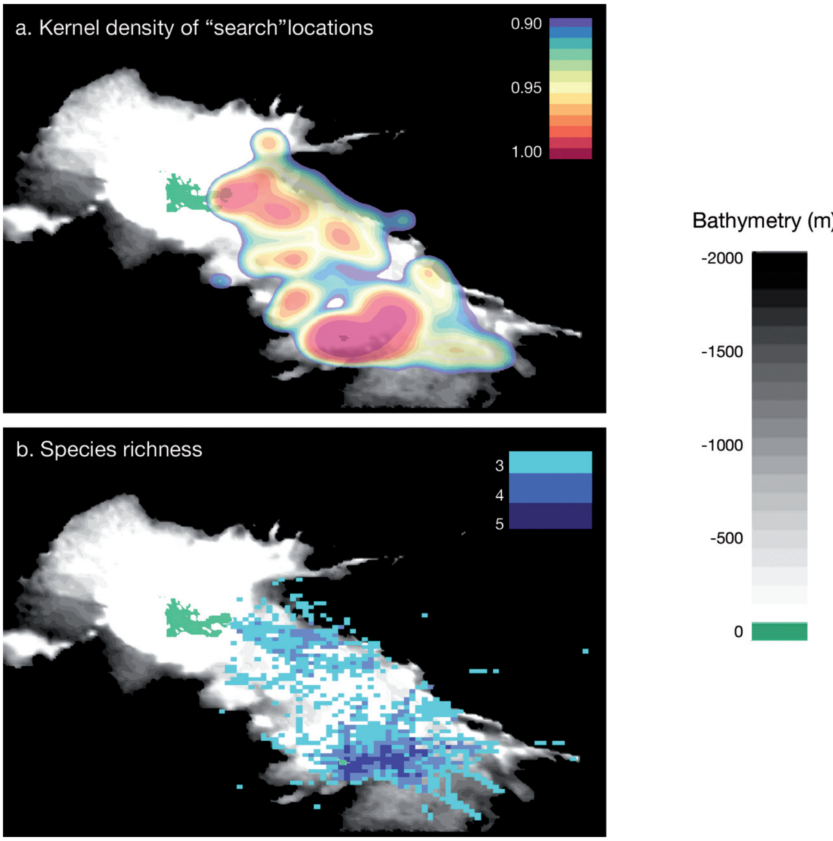

Figure 2. a: Kernel density estimates for all the "search" locations identified by the state space models (all species combined and weighted). b: Species richness in each 10 km^2 grid cell.

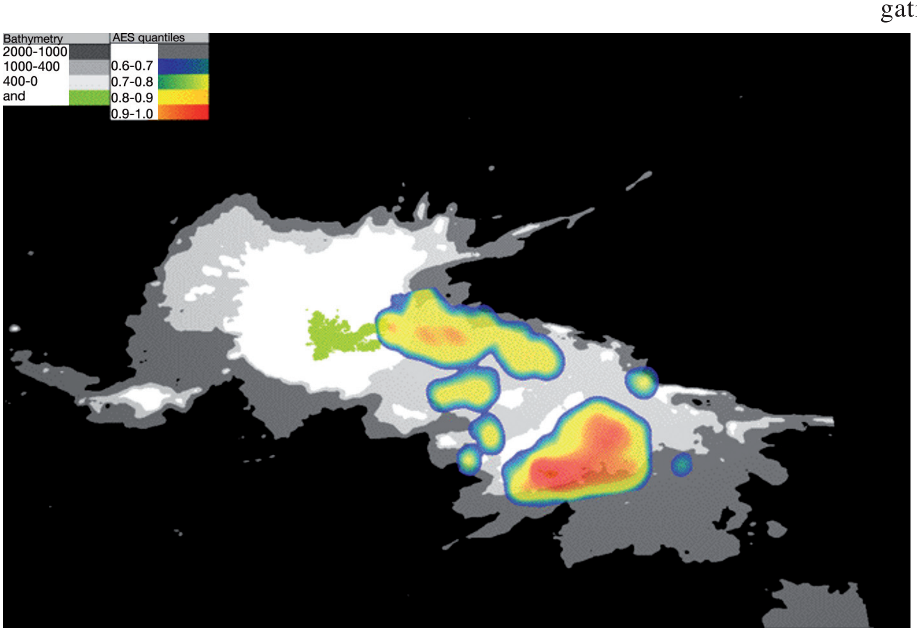

Figure 3. - Kernel density estimates of locations identified as being in an AES.

This is reflected in the very high density of points close to the island (Fig. 1e). By January, the chicks have left the nest and formed *crèches*, freeing both parents to forage simultaneously. During this *crèche* phase, the birds remained at sea for up to a week, and foraged much more widely, and this is when the more distant aggregations of locations are formed.

Areas of Ecological Significance

Multi-species "search" distribution

When locations identified by the SSMs as "transit" mode were removed from the data set, 40 986 locations remained as "search" mode. Once these were subset to provide equal weighting for each species, this was reduced to 26 965 search locations. The outer contour of the resulting Kernel density analysis was almost entirely within the 1000 m bathymetric contour, and indicated foraging locations over most of the southern region of the plateau, from Kerguelen Islands southwards. There were however a number of areas with particularly high densities of locations, the most important extending eastwards from both Kerguelen Islands and Heard Island. No foraging locations were recorded in the northern reaches of the plateau, but there were large aggregations of locations associated with the southern edge of the plateau, and several smaller concentrations at other points on the shelf break and over the plateau itself (Fig. 2a).

Species Richness

The pattern of species richness departed from the pattern above to some degree, most notably the relatively low number of species (three species or less) in the immediate vicinity of Kerguelen Islands. This contrasted with the large number of 10 km^2 cells with four or more species extending east from Heard Island (Fig. 2b). This was not solely due to the fact that fewer species were tagged at Kerguelen Islands (three) compared to Heard Island (five). The region of greatest species richness was associated with the continental slope to the south of Heard Island extending eastwards to Gunnari Ridge. Other regions of relatively high

species richness (cells used by at least four species) were all within the 1000 m contour, and in many cases associated with the steep shelf slope.

Areas of Ecological Significance

The AES were identified by selecting the grid cells with species richness of three or more that also corresponded to high concentrations of locations identified as "search" mode (Kernel density quantiles of greater than 0.90). Fifty-one percent of the combined and weighted locations were considered as being AES, and these occurred in distinct aggregations. The highest concentration of AES locations was associated with the shelf slope south of Heard Island (Fig. 3). The next highest concentration was along the slope to east of Kerguelen Islands. Several other smaller concentrations were also associated with regions of high bathymetric gradients.

Relationship to environmental parameters

Locations of AES were on average, closer to colonies, over shallower water, closer to the 1000 m contour, in slightly cooler water, and associated with slightly higher sea surface height anomalies, than those locations out of AES (Tab. II). However, the distribution of the distance and depth variables were highly skewed and so were log-transformed before inclusion in the GLMs.

The best model describing whether a location was in an AES or not contained all five of the predictor terms (Tab. III), and explained 34.8% of the total model deviance. Based on the ΔAICs, this model performed considerably better than then next model, which included all terms except *dist1000*.

Table II. - Mean (± sd) of model variables for locations defined as either in or out of areas of ecological significance (AES). *Dist0m* = distance to colony (km), *Dist1000m* = distance to the 1000m bathymetric contour (km), *Ocean_Depth* = depth of ocean floor under the grid cell (m), *SST* = Sea surface temperature (°C), *SSHa* = sea surface height anomaly (m).

Model variable	In AES	Out of AES
Dist0m	70.1 ± 64.7	198 ± 101.7
Dist1000m	35.3 ± 26.1	50.5 ± 50.2
Ocean_depth	-469.8 ± 358.1	-1226.0 ± 890.5
SST	3.24 ± 0.66	3.61 ± 1.10
SSHa	6.88 ± 4.51	6.66 ± 4.11

This indicates that each of the terms was having some influence on whether a location was in an AES or not. Distance to the colony (*dist0*), and ocean depth (*Ocean_depth*), were the most influential terms when modelled alone, but addition of the other terms did increase the overall model fit.

The output of the top model was visualised in three dimensions by estimating the likelihood of a location being in an AES based on mean values for *SST*, *SSHa* and *dist1000m,* the three terms with lowest individual model rankings, and a range of values for *dist0m* and *Ocean_depth* (Fig. 4). Under these conditions, the probability of being in an AES increased with diminishing distance to the colony, and increased with diminishing ocean depth.

Three dimensional habitat use

With the exception of Black-browed albatross, all of the species included in this analysis are diving species that

Table III. - Results of logistic general linear models assessing the importance of environmental and behavioural parameters on the likelihood of being in an AES. Listed are the number of terms in the model, the Akaike's Information Criterion (AIC), the delta AIC (ΔAIC) and the percent deviance explained by the model. Terms are as defined in table II.

Model	terms	-Log Likelihood	AIC	ΔAIC	% dev
aes~sst+ssha+dist0m+dist1000m+Ocean_depth	7	-10341.8	20753.9	0	34.7
aes~sst+ssha+dist0m+Ocean_depth	6	-10376.8	20813.8	59.9	34.5
aes~sst+ssha+dist0m	5	-10532.1	21114.3	360.5	33.5
aes~sst+ssha+dist0m+dist1000m	6	-10529.7	21119.6	365.7	33.5
aes~sst+dist0m	4	-10605.8	21251.8	497.9	33.0
aes~ssha+dist0m+Ocean_depth	5	-10873.3	21796.8	1042.9	31.3
aes~dist0m+dist1000m+Ocean_depth	5	-10883.3	21816.9	1063.0	31.3
aes~dist0m+Ocean_depth	4	-10909.8	21859.7	1105.8	31.0
aes~ssha+dist0m	4	-10970.2	21980.5	1226.7	30.7
aes~ssha+dist0m+dist1000m	5	-10966.6	21983.4	1229.6	30.7
aes~dist0m	3	-11023.4	22077.0	1323.2	30.4
aes~dist0m+dist1000m	4	-11021.6	22083.3	1329.4	30.4
aes~sst	3	-15431.4	30893.0	10139.1	2.5
aes~ssha	3	-15830.1	31690.4	10936.5	0.02
aes~dist1000m	3	-15720.5	31471.1	10717.3	0.7
aes~Ocean_depth	3	-13112.5	26255.0	5501.2	17.2
aes~sst+ssha	4	-15420.8	30881.7	10127.9	2.6

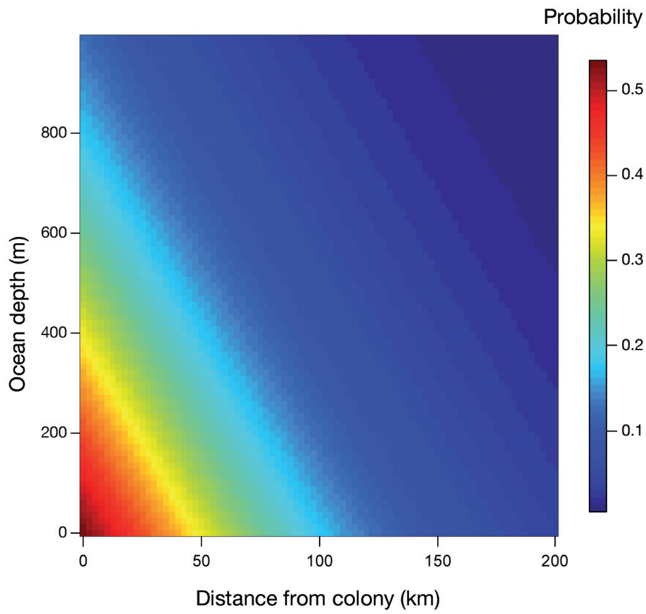

Figure 4. - The probability of a 10 km^2 cell being identified as an AES by the final logistic general linear model. This is illustrated for the two most influential variables in the model (ocean depth and distance for colony), and holding all other variable constant at their mean values.

pursue and catch their prey beneath the ocean surface. Consequently, their habitats should be regarded as three-dimensional rather than two-dimensional as is traditionally the case with tracking studies. We were able to explore this notion as dive data were collected concurrently with the location data for some individuals. Of these species, Elephant seals were clearly the deepest divers, with a mean over all depths of 471 m and mean maximum depths of 1192 m (Tab. IV). Macaroni penguins displayed the shallowest overall depths of 9 m and mean maximum depths of 65.6 m. Antarctic fur seals recorded similar overall depths of 10 m but had deeper maximum depths of 127 m. King penguins had mean depths of 21 m and mean maxima of 198 m. Modal depths revealed a marked contrast between elephant seals and the other species. Elephant seals had a mean modal depth of 446 m, but this value was 0.0 m for all the other species, indicating that they spent more time at the surface than at any other depth. The standard deviation around these estimates was also 0.0 m indicating that this pattern was recorded for all Fur seal, penguin and albatross individuals.

The three-dimensional habitat use was also explored visually, using depth specific kernel densities and iso-surfaces based on the 90% quantiles of these horizontal slices (Fig. 5). For Elephant seals, there are clear differences in the density of locations in different depth slices, which are, to a large extent, associated with bathymetric features such as the shelf slope or sea mounts (Fig. 5). The importance of these deep features for Elephant seals, relative to the other diving species is illustrated by plotting the three-dimensional iso-surface for each species together (Fig. 6). The Elephant seal concentrations are sub-surface and close to bathymetric features, while those for the other species are in the top 100 m of the water column, and although they may be above bathymetric features, individuals are not in direct contact with them.

DISCUSSION

Identifying key foraging habitat is a fundamental requirement for both theoretical and applied ecological studies. High latitude marine ecosystems, however, are particularly difficult to study in this regard due to the logistic difficulties associated with access to these regions for research vessels. Although avian and mammalian predators have the advantage of being relatively visible from ships, synoptic surveys designed to collect the large amounts of data necessary to identify foraging habitats are relatively rare (Peron *et al*., 2010; Woehler *et al*., 2010). An alternative approach is to use tracks of individual animals from telemetry studies to locate regions of high use (Aarts *et al*., 2008; Wakefield *et al*., 2009). Despite recent emphasis on quantifying the at-sea movements of predators, many of which identify areas of concentrated activity for particular individuals (Pinaud and Weimerskirch, 2007; Simmons *et al*., 2007; Shaffer *et al*., 2009), or in some cases populations (Breed *et al*., 2009), there have been relatively few studies that have integrated data from multiple species to achieve a community level assessment of important foraging habitats. This is due in part to the fact that tracking studies have only recently progressed from using small sample sizes to study the movements of individual animals, to incorporating larger, statistically robust samples that can quantify population level habitat use (Morales *et al*., 2010).

This study has demonstrated that multi-species tracking data can be combined to provide new insights into AES for multiple predator populations. Each of the five species included in the study had their

Table IV. - Summary dive statistics for the four diving species. These were calculated from the standardised dive data, with depth values (m) selected every 20 minutes throughout the TDR record. Grand means (± sd) of individual animal dive records (n = 175) for each species are presented.

Species	n	Mean depth	Mean maximum depth	Mean modal depth
King Penguin	34	20.8 ± 7.8	179.5 ± 143	0 ± 0
Antarctic fur seal	47	9.8 ± 5.8	127.0 ± 56.8	0 ± 0
Macaroni Penguin	74	9.4 ± 7.9	65.5 ± 38.5	0 ± 0
Southern Elephant seal	19	471 ± 137.7	1191.9 ± 293.1	446 ± 223

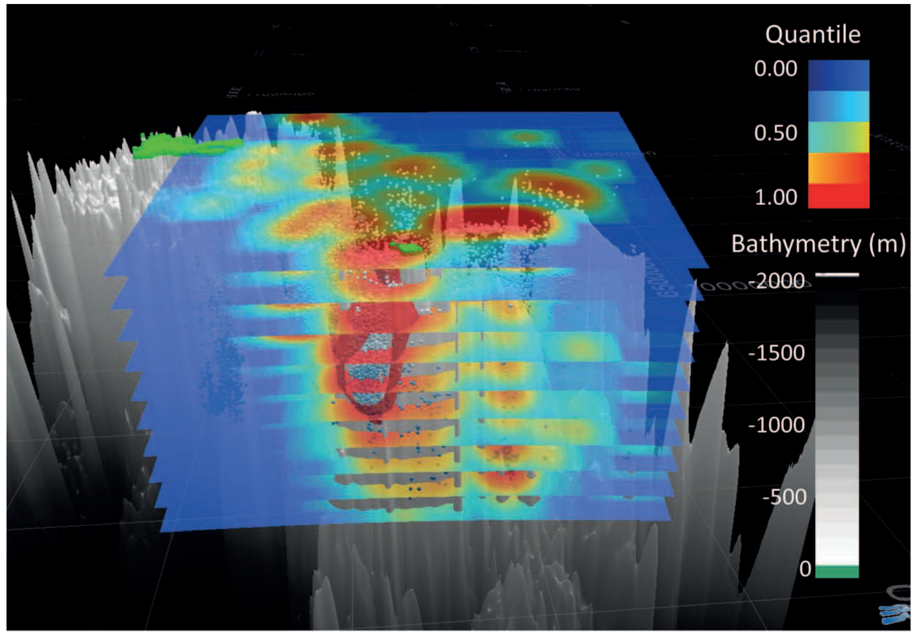

Figure 5. - A three dimensional representation of the foraging space of southern elephant seals over the Kerguelen Plateau. There are 10 horizontal kernel density estimates equally spaced between 0 and 1200 m based on the number of locations in each of hose depth bands.

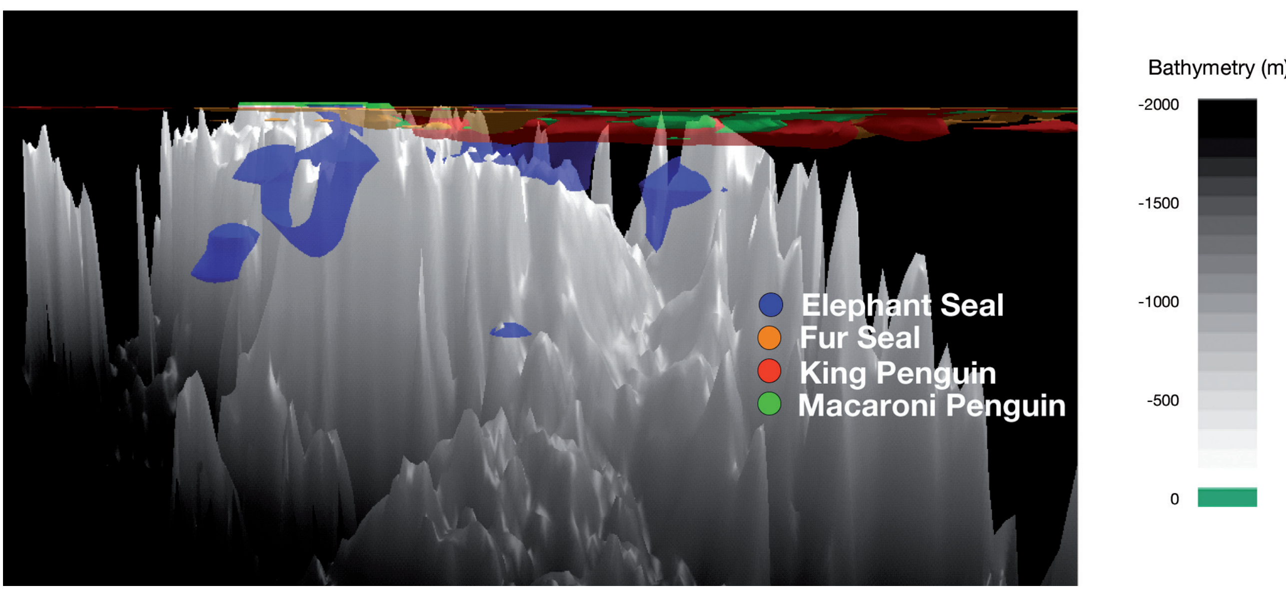

Figure 6. - A three dimensional representation of the foraging space of all four species of diving predators on the Kerguelen Plateau, looking from the west. The distribution of each species is represented by an isopleth enclosing 90% of all diving locations.

own characteristic patterns of foraging locations, which have been described in detail in earlier studies (e.g., Frydman and Gales, 2007). There was however, a tendency for all the species breeding on Heard Island to visit the shelf break to the south and east of the island, and for the Kerguelen Islands animals to disperse in a generally easterly direction. The northwest region of the Kerguelen Plateau was rarely visited; even the Fur seals from Ile de Croy, which had the closest access to this region tended to move westwards and feed off the shelf. These patterns also differed between the islands, and within the islands. This was due to the central place foraging requirements of the species breeding over the summer months, which restricted the foraging trip lengths and therefore the distances that could be travelled. Foraging animals needed to find and exploit the best resources within these constraints (Staniland *et al.*, 2007). Targeting specific features within the foraging range may offer predictable resources providing considerable energetic advantages (Bradshaw *et al.*, 2004). The exception to this was the Elephant seal, which was the only capital breeding species included in the study (see Houston *et al.*, 2007). Only a proportion (approximately 40%) of the sub-adult male popula-

tion remained over the Kerguelen Plateau, while the remainder dispersed more widely throughout the Southern Ocean (Bailleul *et al*., 2007a; Bailleul *et al*., 2007b).

An important feature of our analysis was the combination of data from several years which incorporated inter-annual variability in foraging locations among the species. There is sufficient complexity in the bathymetry of the Kerguelen Plateau that oceanographic features, such as the extent of Polar Frontal Zone, differ in both their location and strength between years (Park *et al*., 2009; van Wijk *et al*., 2010; Park and Vivier, 2011), and this is reflected in shifts in the foraging areas of predators such as Antarctic fur seals (Lea *et al*., 2008). Such variability affects areas of species richness and AES both within a season and between years, and highlights the need to include multiple years of study for each species in order to ensure the AES include the full range of likely foraging areas. While this level of temporal coverage was available for Antarctic fur seals from Kerguelen Islands, for most of the species in our study, there was only a single year of data from each site. Expanding the temporal coverage for these species is needed before AES can be properly described for the Kerguelen Plateau. Here, we have defined AES as those regions with high numbers of non-transit locations that also displayed high levels of species richness. This definition has the advantage of removing the over-emphasis of locations associated with migratory paths, which inevitably cluster around colonies, at least for central place foragers. Animal movement models are increasingly being used to identify 'foraging' regions along a track, as the slow travel and high turning rates are assumed to be associated with searching for prey (Jonsen *et al*., 2005; Breed *et al*., 2009). Independent validations of this assumption have been few, for example, Thums *et al*. (2011), found that southern elephant seals tended to gain condition when inside search zones identified by first passage time analysis. This is not always the case however, as juvenile southern Blue fin tuna (*Thunnus maccoyii* Castlenau, 1872) actually fed less often in areas where they tended to spend the most time (Bestley *et al*., 2008; Bestley *et al*., 2010).

By incorporating species richness, we single out regions that are important to multiple predators. These areas will be particularly ecologically important as they must be regions with high diversity of prey species. The five species incorporated in this study feed on a range of prey species, although there is undoubtedly an overlap in their diet; for example, all species but the albatrosses are known to feed on myctophid fish (Cherel *et al*., 2010). Despite this, each species occupies its own dietary niche, so aggregations of different predators, within the constraints imposed by breeding schedules and feeding of young, are likely to be associated with a particularly diverse or predictable abundance of a range of prey species.

As this analysis is primarily a "proof of concept", and only used a fraction of the available tracking data, we have not likely captured all the potential AES within the region surrounding Heard Island and Kerguelen Islands. However, the very fact that there are regions that were commonly used by at least three species is a significant step in our understanding of the ecosystem of the region. The analyses reveal two principal AES, one to the east of Kerguelen Islands, lying within and parallel to the eastern 1000 m contour and its associated steep slope. The other was again associated with the 1000 m and steep slope, but to the south and east of Heard Island.

The general linear models indicated that all five habitat and environmental variables contributed to explaining whether a location was classified as an AES. However, the most influential of these individually were distance to the colony and ocean depth, reflecting the tendency of the animals to remain over the shelf and forage close to the breeding colonies during the breeding season. This highlights the strong seasonal aspect to habitat use in these species, and it is likely that AES will be very different outside the breeding season, when adults are not regularly feeding their offspring. Studies of winter foraging of these species have commenced in recent years and in each case foraging ranges extend well beyond the Kerguelen Plateau (Charrassin *et al*., 2008; Bost *et al*., 2009).

Nonetheless, the AES are not determined solely by the breeding biology of the predators; distribution and abundance of the prey are also likely to be influential. As with most studies of marine predators, direct measures of the prey field are impractical (Hindell, 2008), and so remotely sensed ocean parameters which are known to influence primary productivity, such as SST and SSH are used as an approximation (Cotté *et al*., 2007; Simmons *et al*., 2007). While both of these variables were included in the final model, indicating that they did have some influence on whether or not a cell was considered an AES, their importance was relatively minor. There are several likely reasons for this. Sea surface height and temperature may not have been the most appropriate variables, particularly as the animals were concentrating their foraging over the shelf and the shelf breaks, where local upwellings may not be characterised by these variables. Sea surface colour, a measure of Chlorophyll-a concentrations in the surface waters, may provide a better measure. However, extensive and persistent cloud cover in the region meant that these data were too sparse for use in our study. Further, there may be spatial and temporal mismatches between the physical oceanographic properties of the ocean and the distribution of the prey of predators (all of which are meso-predators of euphausiids, myctophids and squid).

Satellite products only provide data pertaining to the ocean surface, while prey are distributed throughout the water column, and this vertical distribution is determined by

factors that may not be detectable in surface-measured variables (Biuw *et al*., 2007). For example, the AES associated with Heard Island, encompassed the shelf slope south of the island extending north-westward to Gunnari Ridge. Shelf slopes are often associated with upwellings or other ocean processes, leading to enhanced prey availability (Bost *et al*., 2009). A large proportion of the Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898) caught by commercial fisheries in the Kerguelen Plateau region are from the slopes (Lord *et al*., 2006). The Elephant seals in this study also showed a strong tendency to forage over the slopes, often diving to the sea floor. Adult female Elephant seals from Kerguelen Islands, are also known to feed on myctophids (Ducatez *et al*., 2008); however there are few data on the diet of the juvenile males that constituted the bulk of the animals in this study. Despite the importance of the southern shelf slope to the predators from Heard Island, neither SST or SSH were strong indicators of AES in the region. Developing a well-parameterised model that describes AES in the region remains an important challenge for future studies.

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